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On the Nature of Production in the Sea

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INTRODUCTION AND ESTIMATION OF PARAMETERS

THE production of living matter in the sea is based on the production of algae. This may be formulated as follows:—

$$\frac{dP}{dt} = P(R - M - G)$$

where P is the number of algae (or weight of carbon) per unit volume or beneath unit surface;
R is the instantaneous reproductive rate of the algae;
G is the instantaneous mortality rate due to grazing;
M is the instantaneous mortality rate due to 'natural' causes.

As R and G are not the same throughout the season, the course of production is best dealt with in weekly stages, e.g.:—

$$P_1 = P_0 \cdot e^{(R_0 - M_0 - G_0)(t_1 - t_0)};$$

$$P_2 = P_1 \cdot e^{(R_1 - M_1 - G_1)(t_2 - t_1)};$$

where the first week is represented by the time from t_0 up to t_1 and the second week by the time from t_1 to t_2; P_0, P_1 and P_2 are the numbers of algae at times t_0, t_1 and t_2; R_0 etc., and R_1 etc., are the exponents in the first and second weeks respectively.

Each parameter is difficult to estimate; we may consider them as follows.

1. P, THE NUMBERS OF ALGAE

The numbers of algae may be estimated by net hauls, chlorophyll estimates or by sedimentation from a preserved water sample. A net haul underestimates the population by up to one hundred times, because the cells go through the meshes (Steemann Nielsen, 1938). Chlorophyll measurements may overestimate the population by up to five times, because some dead chlorophyll has passed through the guts of herbivores (Gillbricht, 1952). Cells counted by the sedimentation method are measured for size and by combining size and numbers, an estimate of algal volume in μ^3 is made. This method is laborious but is the most reliable so far for temperate waters during the spring outburst; in other regions or in the summer of temperate regions and particularly in coastal waters, μ-flagellates are sometimes important, which cannot be estimated by the sedimentation method.

2. R, THE REPRODUCTIVE RATE

The reproductive rate may be estimated indirectly by measuring photosynthesis either by the oxygen method (Gaarder and Gran, 1927) or by the C^{14} method (Steemann Nielsen, 1952) or directly, using the cell-size decrease method (Cushing, 1955).

By means of the cell-size decrease method, the number of divisions can be estimated between two times of observation in the sea; it is however only applicable to diatoms in the

open sea and the diatom populations must be identified as being the same between the two times of observation. The photosynthetic methods both require an estimate of the standing stock of carbon, which can be obtained from the algal volume in μ^3, using the algal volume/carbon ratio (Cushing, 1957a). Practically, the best method is to combine the cell-size decrease method with one of the photosynthetic methods, in some way, because in the former method the effect of vertical turbulence is taken up and in the latter all forms of algae are represented.

3. *M*, THE 'NATURAL' MORTALITY RATE

An estimate of this factor has been made (Cushing, 1955) from the counts of empty diatom frustules. From Apstein's work on dead diatoms, showing that they sank at about 10 to 15 m/day, it was assumed that any count should be divided by the number of days to sink to the bottom. In this way the mortality amounted to about 1%; as this is an overestimate, it will be subsequently discarded for the present study of spring production in temperate seas, although there may be situations in which 'natural' mortality is the dominant factor.

4. *G*, THE MORTALITY RATE DUE TO GRAZING

$$G = R - \frac{1}{t_1 - t_0} \cdot \log_e \frac{P_1}{P_0}$$

Estimating the grazing mortality in this way, we depend entirely upon the reliability of the other estimates, *R* and *P*. Another test is to find out whether the herbivores get enough to eat.

Riley (1946) assumed that $G = gZ$, where Z is the quantity of zooplankton and g is a constant expressing their minimal need for food, which is 1·3 to 7·6% of their carbon content per day; throughout the year, *on the average*, this corresponds to 63 mls 'swept clear' per mg wet weight of zooplankton (Riley, Stommel and Bumpus, 1949). For *Calanus* V the minimal need is worked out as follows:—

A	*B*	*C*	*D*
Wet weight mg.	*Dry weight* ($A \times 1/9$) *mg.*	*Daily need of dry weight* (5% *of B*) *mg.*	*Daily need of wet weight* ($C \times 9$) *mg.*
0·59 (Bogorov, 1939)	0·065	0·0033	0·03

Off the north-east coast of England in 1949, at the very peak of plankton production, the algal stock was 0·5 mg wet weight/litre; so, even then, one *Calanus* V must have 'swept clear' $\frac{0{\cdot}03}{0{\cdot}5} \times 1{,}000 = 60$ mls/day in order to survive. Before and after the peak, the volume swept clear must have been very much higher.

Experimental observations on grazing depend on the following formulation:—

$$G = -\frac{1}{t} \cdot \log_e \frac{P_1}{P_0},$$

$$F = GVt$$

where V is the volume per animal, in mls;
where F is the 'volume swept clear', in mls.

In some experiments, a control has been used and in others the experiments were carried out at short time intervals (for example, 7 hours). The observations of 'volume swept clear' for *Calanus* V and ♀ range from 1 to 240 mls/day, the majority being from 1 to 60 mls/day.

There is thus a discrepancy between the experimental values of grazing in mls/day, which range from 1 to 60 mls/day, and the minimal daily need in mls/day, which is greater than 60 mls/day. Recent experiments (Cushing, 1957c) have shown that the discrepancy is possibly resolved; it was shown that the 'volume swept clear' increased as the volumes of experimental vessels were increased:—

Volume of vessel	5 *ml.*	25 *ml.*	100 *ml.*	500 *ml.*
Volume swept clear by *Temora longicornis* in one day	6 ml.	13 ml.	26 ml.	150 ml.

With *Anomalocera patersoni*, using 2–5 litre flasks, grazing rates of 800–1,200 mls/day have recently been obtained.

In the present paper, an attempt will be made to construct a model of the spring outburst of plankton production, using theoretical reproductive and grazing rates.

I. THE DEVELOPMENT OF A SIMPLE MODEL OF PLANKTON PRODUCTION IN TEMPERATE SEAS

I. (i) ON THE ALGAL DIVISION RATES

A theoretical algal division rate depends upon the relation between reproductive rate in the euphotic zone to the energy reaching it. To do this, experimental observations made by Lund (1950) on the freshwater diatom, *Asterionella formosa* Hass. will be used together with those of Jenkin (1937) on the marine diatom, *Coscinodiscus excentricus* Ehr.

Cultures of *Asterionella* were suspended by Lund in Windermere at 0·5 m, 5m and 7m for weekly periods from February to December. He was able to measure the number of divisions that had taken place in each week. Light intensity was recorded as kilolux hours ashore with a 'barrier relay' photocell. Luxes may only be directly converted to energy at a wavelength of 560 mμ (millimicrons), at which 1 g cal/cm^2/hr = 7·75 kiloluxes (Sverdrup, Johnson and Fleming, 1942). However, Sverdrup *et al.* suggest that at the surface of the water luxes be multiplied by 1/0·15 to give g cal/cm^2/hr. The energy received at the surface must be reduced by the energy extinction coefficient appropriate to the water type in the lake. Pearsall and Ullyott (1934) made careful observations of light penetration into Windermere, using an opal and a blue-green filter (Wratten 1949, with maximum transmission at 545 mμ and spectral range from 360–700 mμ); they found that the percentage transmission was 37%/m. If it is permissible to use this observation to classify the water type (Jerlov, 1951), then the water in Windermere could be described as 'coastal water 9'. Jerlov has tabulated energy extinction coefficients for different water types at a series of depths. The value of energy in g cal/cm^2/min at the depths at which the culture bottles were suspended, is increased by 30% to allow for scattering of light into the culture bottles from angles other than the vertical (Jerlov, 1951).

In order to calculate the energy reaching the three culture depths, 0·5 m, 5m and 7m, throughout the day, account must be taken of the sun's altitude. The energy reaching a given depth at a given time is derived with the use of the following formula:—

$$\frac{1}{\sin a} \cdot d. \sin a_t ,$$

where a is the sun's altitude at midday, a_t the altitude at any other time and d is the depth of any percentage of energy penetration at midday. So, considering a constant depth, the energy in g cal/cm²/m reaching that depth in each hour may be calculated; these values are then summed for the whole day at that depth. This procedure was carried out for each week from January to June for coastal water 9 at 0·5 m, 5 m and 7 m.

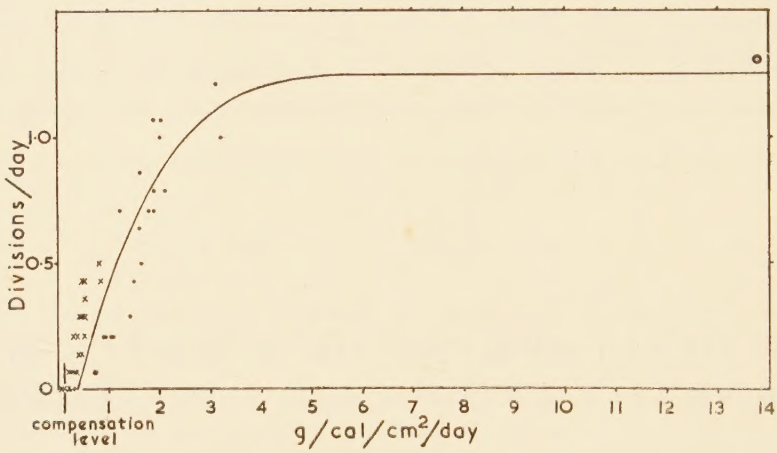

FIG. 1. *Division rates of* Asterionella formosa, *Hass. Related to radiant energy. (from Lund's* (1950) *data).*
Circle indicates observations at 0·5 *m (averaged), dots those at* 5·0 *m and crosses those at* 7·0 *m.*

Figure (1) shows the results from Lund's experiments, where the number of divisions/day of *Asterionella formosa* is plotted against g cal/cm²/day at the depth at which the culture bottles were suspended. Only the observations for 5 m and 7 m were used because many of those at 0·5 m would probably be at the inhibition level of radiation. The best fitting line to the points was drawn by eye. It intersects the x-axis at 0·4 g cal/cm²/day, which is not very different from the value found at the compensation depth (Jenkin, 1937, quotes 0·13 g cal/cm²/hr at the compensation depth, where the 'day' may be as short as three hours).

It is now necessary to estimate the average daily input of energy into the sea each month in the central North Sea. The average radiation reaching the sea surface in Lat. 52°N, expressed in g cal/cm²/min, is given in Sverdrup *et al* (Table 25). The duration of daylight on the 15th of each month from January to June was taken from the Nautical Almanac (1953). When the sun is low in the sky much of its energy is reflected; Table 26 in Sverdrup *et al* gives the percentages of energy reflected at different altitudes. From the calculated time spent by the sun at different altitudes, the length of day was corrected to apparent hours of daylight just below the surface of the water, taking into account the proportion of energy lost by surface reflection.

The energy reaching just below the surface throughout the day on the 15th of each month from January to June has been calculated. The mean energy reaching certain depths

can be calculated, using the energy extinction coefficients for coastal water Type 1 (Jerlov, 1951), which is that usually found off the north-east coast of England; the values for each month from January to June are given in Table I.

TABLE I

Average energy in g cal/cm²/day in Lat. 52°N, January to June, reaching the surface and reduced by the energy extinction coefficient of coastal water Type I (of Jerlov, 1951)

	January	*February*	*March*	*April*	*May*	*June*
Surface	18·98	44·91	92·09	164·25	219·20	242·06
1 m.	7·00	16·57	33·98	60·61	80·88	89·32
2·5 m.	4·50	10·64	21·83	38·93	51·95	57·37
5·0 m.	2·70	6·38	13·08	23·32	31·13	34·37
7·5 m.	1·71	4·04	8·29	14·78	19·73	21·79
10·0 m.	1·12	2·65	5·43	9·69	12·93	14·28
12·5 m.	0·80	1·89	3·87	6·90	9·21	10·17
15·0 m.		1·35	2·76	4·93	6·58	7·26
17·5 m.		0·90	1·84	3·28	4·38	4·84
20·0 m.			1·20	2·14	2·85	3·15
22·5 m.			0·83	1·48	1·97	2·18
25·0 m.				1·15	1·53	1·69
27·5 m.				0·82	1·10	1·21
30·0 m.					0·66	0·73

Note: The effect of different altitudes of the sun in reducing these quantities is not taken into account in the figures given in Table I.

To obtain the total energy reaching each depth throughout the day, the values of the average daily energy reaching each depth, given in Table I, must be corrected for the changes in the sun's altitude by the formula given above.* Then using the relation given in Figure 1, an average expected division rate for the euphotic zone is obtained from the daily energy reaching each depth. A specimen calculation is given below:—

January 15th

Depth m.	*Time G.M.T.* 0900	1000	1100	1200	*g.cal/cm²/d*	*Divs/day (Fig. 1)*
2·5	0·280	0·560	0·640	0·680	3·64	1·17
5·0	0·098	0·280	0·365	0·410	1·89	0·82
7·5		0·160	0·220	0·260	1·02	0·42
10·0		0·093	0·140	0·170	0·64	0·19
12·5			0·100	0·120	0·32	
				Average division rate/day	.	*0·65*

*It must be pointed out that the effect of the sun's altitude is not taken into account in estimating the energy reaching the sea surface.

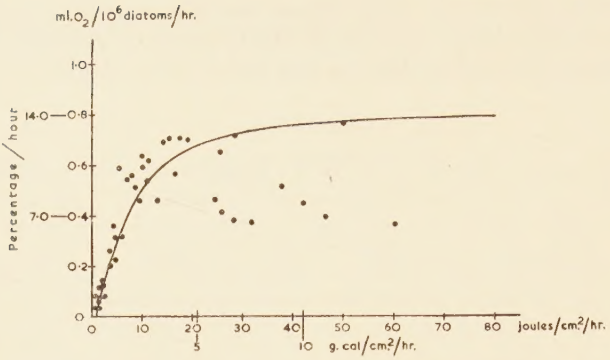

FIG. 1a. *Percentage production and energy (from Jenkin's Figure* 9).

In May the average expected division rate/day would be 0·97. This may be compared with another estimate made using Jenkin's results (1937); her Figure 9 summarizes most of her results and is reproduced here as Figure (1a). There are two modifications to the original figure, firstly the ordinates are expressed in a scale of percentage production of oxygen per hour per 10^6 diatoms (*Coscinodiscus excentricus*) and, secondly, the abscissae are expressed as g cal/cm²/hr. Taking the average energy input in g cal/cm²/hr at various depths in May and the length of day at those depths, the following table is constructed.

Depth m.	*g.cal/cm²/hr*	*k: % increase in oxygen production/hr*	*time in hrs* (t)	*The daily % increase* (e^{kt})
2·5	2·50	9·0	16	326
5·0	1·50	6·8	14	158
7·5	1·02	5·1	12	84
10·0	0·64	3·4	12	51
12·5	0·50	2·7	10	31
15·0	0·38	1·7	8	13
17·5	0·27	1·5	6	9·5
20·0	0·19	1·0	4	4·0
			Average	85

Expressed as a reproductive rate, this average percentage increase of 85% would be 0·85, which compares quite well with that of 0·97, obtained by the other method.

So far, no account has been taken of vertical mixing. If a diatom spends only half the day in the euphotic zone, then the average division rate is halved. It was assumed that Ekman's depth of frictional resistance was a good estimate of the depth of vertical mixing. For wind velocities below 6 cm/sec, Thorade's formula was used:—

$D = \frac{3{\cdot}6W^3}{\sin \phi}$, where D is the depth of frictional resistance in m, ϕ is the latitude in degrees and W is the wind strength in m/sec. For wind velocities above 6 cm/sec, Ekman's formula was used: $D = \frac{7{\cdot}6\,W}{\sin \phi}$. From the hydrographic charts issued by the International Council for the Exploration of the Sea, mean wind strengths in the central North Sea were tabulated as average velocities in mph from January to June, inclusive, from 1950–1953.

The compensation depth varies throughout the day with the sun's altitude, but the depth of mixing remains roughly constant. So the ratio of compensation depth to the depth of mixing increases up till midday. The ratio is averaged for the whole day in the following way:—

January: Apparent dawn 0830 *hours*

Time (G.M.T.)	0800	0900	1000	1100	1200
Compensation depth D_c (m)	—	4·3	8·5	10·6	11·9
Depth of mixing, D_m (m)	—	55·4	55·4	55·4	55·4
Ratio; $\frac{D_c}{D_m}$		$\frac{2\left(\frac{4\cdot3}{55\cdot4}\right)+2\left(\frac{8\cdot5}{55\cdot4}\right)+2\left(\frac{10\cdot6}{55\cdot4}\right)+\frac{11\cdot9}{55\cdot4}}{7}=0\cdot151$			

Note: The apparent dawn is the time at which the sun's rays first penetrate the surface.

Table II gives the depth of frictional resistance, D_m, the compensation depth D_c, the ratio D_c/D_m, the estimated division rates in the euphotic zone R_p, and the estimated division rates in the whole water column, R. These are the division rates on which the operation of the plankton model depends.

TABLE II

Derivation of the theoretical division rates of the algae

	January	*February*	*March*	*April*	*May*	*June*
D_c at midday, m.	11·9	17·0	19·5	22·0	23·2	23·3
D_m, m.	55·4	57·0	40·2	37·2	29·8	30·2
D_c/D_m	0·151	0·201	0·321	0·394	0·521	0·505
R_p	0·65	0·73	0·88	0·98	0·97	0·97
$R_p \times D_c/D_m = R$	0·098	0·147	0·282	0·386	0·505	0·490

A check on the theoretical division rates is provided in the following way. Off the north-east coast of England in 1949 (Cushing 1955), using the cell-size decrease method in April, an average division rate of 0·43 was obtained. The value in April given in Table II is 0·386; the agreement is good considering that the theoretical value is derived from average energy inputs and average wind speeds.

I (ii) ENCOUNTER THEORY OF GRAZING

It has been shown above that *Calanus* V must sweep clear more than 60 mls/day in order to survive for most of the year in the North Sea. Further, it was shown that volumes swept clear of 800–1,200 mls/day have been obtained by experiment. This is much greater than any quantity that might be obtained by filtering in a normal enviroment. They might however obtain this quantity by encounter. It must be a strictly tactile encounter because it has been shown that *Calanus* guts are full in darkness, both in the sea and during laboratory experiments (Wimpenny, 1938; Gauld, 1951).

Copepods move forwards with the antennules extended and any diatom would be caught on the hairs projecting from them. Perceived in this way, the diatom is then seized and eaten. Then the 'volume swept clear' in barren water would be the volume swept during 24 hours by this tactile apparatus on the moving copepod. If there are diatoms in

the water, the animal stops to feed, reducing the volume that would have been swept in barren water. Some very small organisms might be directly swallowed while the copepod is actually moving, but the mass of such organisms is small and it is thought that they would not have any substantial effect on the encounter theory.

Let c be the area of the surface described by the hairs projecting from the antennule in the plane normal to the direction of movement—the contact surface. Let d be the average distance travelled in one day by the copepod. Then $cd = S_m$, the 'mechanical' volume swept clear in barren water, in mls/day. Let x be the time in seconds to eat one diatom of a given volume in μ^3 (10,000 μ^3). Let y be the number of diatoms of that volume in each millilitre, and that all diatoms are of that volume. Let v be s_m/sec.

It takes x seconds to capture and eat one diatom and $x.y$ seconds to capture and eat the diatoms in 1 millilitre.

In one second the animal sweeps clear 'mechanically' v mls (S_m/sec) and so it takes $v.x.y$ secs to capture and eat the diatoms contained in v mls.

Therefore it must take $1 + v.x.y$ days to capture and eat the diatoms in S_m mls; consequently in one day the 'operational' volume swept clear, S_0, is $\frac{S_m}{1 + v.x.y}$ mls/day.

This expression gives weight to the fact that a copepod cannot start to eat a second diatom during the time in which it is eating the first.

In order to use this formula, information is needed on the sizes of copepods, the lengths of their antennules and of the projecting hairs. From Sars' '*Crustacea of Norway*', a number of measurements of original drawings were made; it was observed that, in general, the antennule was about 7/6 of the body length; also, that the antennule hairs of *Calanus* were about one quarter of the antennule length, but that this ratio was one tenth for the other copepods. Measurements of copepods were given in Cushing (1955) in the following categories: *Calanus* copepodite stages I, II, III, IV, V, VI, *Pseudocalanus*, *Paracalanus* and *Temora* (the three latter include adults and copepodite stages).

Information is also needed on the distances moved in each day in barren water. This was taken from the literature on vertical migration; it was assumed that the speed from the depth reached at midday to the depth reached by sunset was a good estimate of speed through barren water, because much of this migration takes place below the euphotic zone. In other words, animals would be climbing into the euphotic zone from below and their speeds would be reduced by the presence of food only towards their end of their migration. Yet this may well be an underestimate, because it is tacitly assumed that the animals move in straight lines. The published results used for this estimate were for: *Daphnia longispina* (Southern and Gardiner, 1932; Worthington, 1931); *Temora* (Savage, 1926); *Eurytemora grimmi* (Bogorov, 1939); *Calanus* (Esterly, 1912; Savage, 1926; Nicholls, 1933; Hardy and Gunther, 1935; Clarke, 1933; Farran, 1947); *Metridia* (Esterly, 1912; Clarke, 1936);

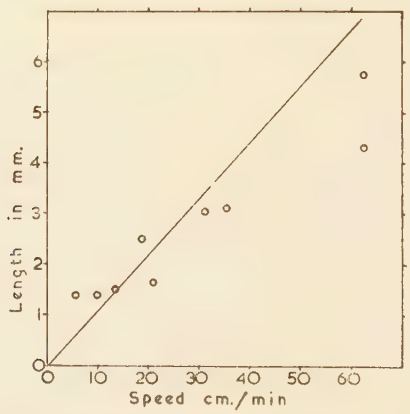

FIG. 2. *Relation between length and estimated average speeds of certain plankton animals.*

Diaptomus (Worthington, 1931; Ullyott, 1939); *Euphausia superba* (Fraser, 1936). Length measurements of copepods were taken from Sars' '*Crustacea of Norway*'; the length of *Daphnia hyalina* Leydig was estimated from fifty measurements made in Windermere by me in 1952; the mean lengths of calyptopis I, II and III and furcilia I of *Euphausia superba* were taken from Ruud (1929). Mean lengths are plotted against mean speeds in Figure (2); a line has been drawn to the points through the origin. So for a given length in cm an average speed in cm/min can be obtained.

The information gathered can now be combined to calculate S_m, the 'mechanical' volume swept clear. A sample calculation is given in Table III for the common copepod categories in the central North Sea. Lengths are given from the quoted sources; from Figure (2) the average speeds are calculated. The antennule and hair measurements are given from which the contact surface is calculated. Contact surface multiplied by the distance travelled in one day gives S_m.

TABLE III

Derivation of S_m, the 'mechanical' volume swept clear

	Length (*cm*)	*Speed* (*cm/min*)	*Antennule* (*cm*)	*'Hairs'* (*cm*)	S_m *ml/sec*	S_m *ml/day*
Calanus VI . .	0·352	32·2	0·41	0·10	0·0455	3931
Calanus V . .	0·306	28·0	0·36	0·09	0·0295	2549
Calanus IV . .	0·232	21·2	0·27	0·07	0·0128	1109
Calanus III . .	0·176	16·0	0·21	0·05	0·0055	475
Calanus II . .	0·123	11·0	0·14	0·036	0·0018	158
Calanus I . .	0·088	8·0	0·10	0·026	0·0007	58
Pseudocalanus .	0·130	11·7	0·15	0·015	0·0008	72
Paracalanus . .	0·098	8·7	0·11	0·011	0·0003	29
Temora . .	0·143	13·0	0·17	0·017	0·0012	101

From Table III, length in cm has been plotted against S_m, the 'mechanical' volume swept clear, on a log/log plot. This is because S_m is obtained by multiplying the contact surface in cm^2 by the distance in cm/day and because over a limited range, length is proportional to speed or distance/day. The values of length and S_m given in Table III

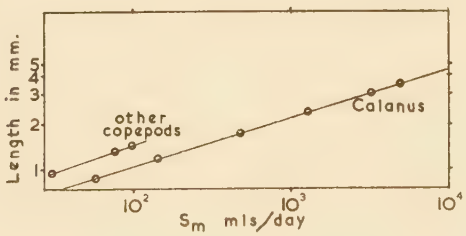

FIG. 3. *Mechanical daily grazing rates for* Calanus *and 'other copepods'.*

are plotted in Figure (3); the difference between the lines for *Calanus* and the 'other copepods' is due to the relative differences in contact surfaces.

Information on the time to eat diatoms can be calculated from certain grazing experiments (Harvey, 1937, on *Ditylum*, *Lauderia* and *Nitzschia*; Gauld, 1951, on *Chlamydomonas*; Marshall and Orr, 1955, on *Chaetoceras*). The time to eat one diatom, x, was calculated from $S_0 = S_m/1 + v.x.y$.

$$\text{i.e., } x = \frac{1}{v.y}\left(\frac{S_m}{S_0} - 1\right).$$

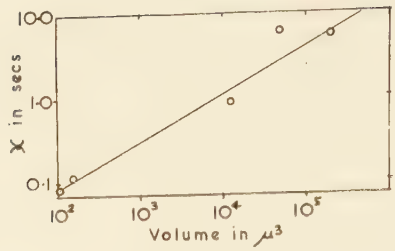

FIG. 4. *Relation between the estimated time to eat one diatom (x) and the volume of the diatom in* μ^3.

S_m was taken from Table III; S_0, the 'operational' volume swept clear, was calculated from the published data using the formula given above. The estimated time to eat one diatom is plotted against the observed sizes of diatoms in Figure 4, on a log/log plot. It is assumed that there are two distinct actions, capture and ingestion. The time to capture is probably inversely proportional to the size of the diatom, because the size of diatoms is inversely proportional to their numbers per unit volume. The time to ingest a diatom is probably directly proportional to size. Figure (5) shows the experimental observations used as values of S_0, the operational volume swept clear, at different densities of diatoms in numbers. It is clear that a certain order has imposed upon the results of a diverse series of experiments.

The encounter theory of grazing, which states that copepods obtain their food by tactile encounter as they move steadily through the water, has not been confirmed in detail. However, Ryther (1954) has published details of experiments on the apparently inhibitory effect of phytoplankton on the feeding of *Daphnia magna*. His observations were compared with the calculated values, using the encounter theory of grazing. From measurements of *Daphnia magna*, a contact surface of 0·75 mm² was measured; from Worthington (1931) and Pennak (1944) an average speed of 0·185 cm/sec was estimated. Table IV gives a comparison of Ryther's observed values and those calculated, using the encounter theory of grazing.

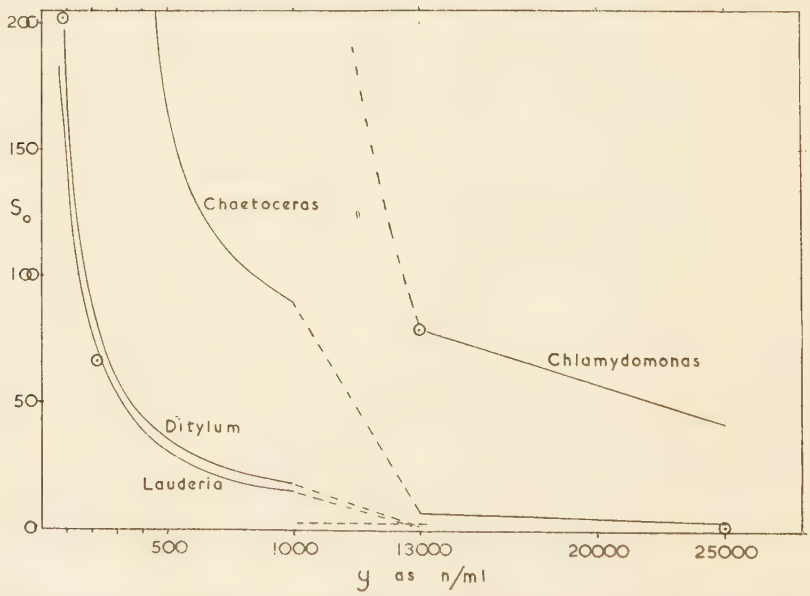

FIG. 5. *The value of* S_0 *under different experimental conditions of size and density of diatoms (from the data of Harvey,* 1937, *and Gauld,* 1951).

TABLE IV

Comparison of Ryther's observed values of volume swept clear with those calculated from the encounter theory of grazing Chlorella

number/mm³	*Observed volumes swept clear in mls/day*	S_0; *the operational volume swept clear in mls/day* $x = 1{\cdot}1$ sec (*diatom of* 10,000 μ^3)	$x = 0{\cdot}008$ sec (*diatom of* 10 μ^3)
20	4·17	3·86	3·23
40	4·06	3·12	2·37
80	3·84	2·26	1·55
120	3·65	1·77	1·15
160	3·47	1·41	0·91
200	3·30	1·24	0·76
240	3·20	1·07	0·65

The correspondence between theory and observation is not very good, but considering the possible range it is remarkably close. The apparent inhibition with increasing algal numbers is probably not a direct one, but merely a function of the time it takes *Daphnia* to eat *Chlorella*, or *Scenedesmus*. It is likely that the time to eat one *Chlorella* is overestimated, because the value is taken from largish diatoms, whereas *Chlorella* can only be filtered. So the calculated decrease in S_0 with algal density is much too great.

Combining this test with the experiments showing high grazing rates given above it is considered that the encounter theory of grazing may be used in the construction of the model of plankton production. This is done in the following way. From the Flamborough Line material, numbers/m³ of *Calanus* copepodite stages I–VI and 'other copepods' (*Paracalanus*, *Pseudocalanus*, *Temora*, *Acartia* and *Oithona*) are available for each month. From the distribution of numbers of *Calanus* stages an average value of S_m for each month was

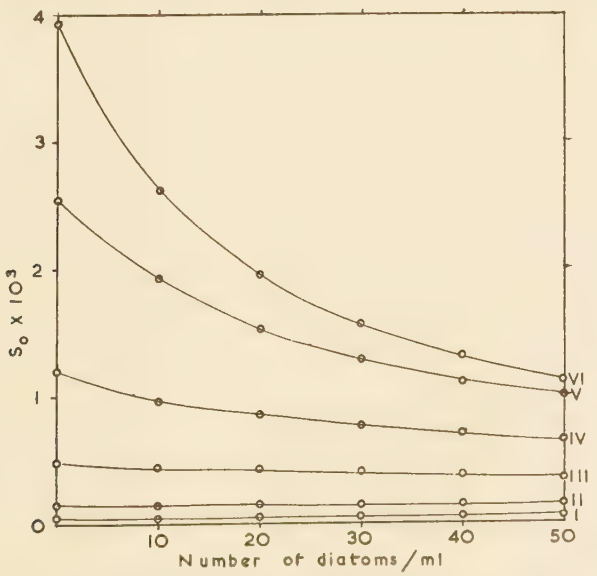

FIG. 6. *Relationship between S_0 and the number of diatoms per ml for the six copepodite stages of* Calanus.

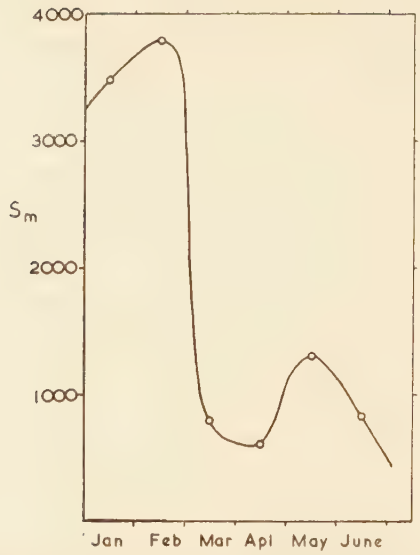

FIG. 7. *Estimated values of S_m from the size distribution of the Flamborough Line Material* (1947-50).

calculated (Figure 6). Values of S_0, the operational volume swept clear, were also calculated for a range of algal numbers, at a constant algal size of 10,000 μ^3. These calculations are shown graphically in Figure (7). Similar calculations were made for 'other copepods'. For the actual operation of the plankton model weekly values of S_m were interpolated from Figure (7) for *Calanus*; for 'other copepods' a standard value of 70 mls/day was taken. The weekly values are given in Table V.

Using the weekly value of algal numbers, S_m is converted to S_0. The S_0 for *Calanus* is multiplied by the number of *Calanus*/litre in that week; similarly for 'other copepods'. The

TABLE V

Weekly values of S_m, the mechanical volume swept clear, for Calanus *and 'other copepods', in mls/day*

	January				*February*			
	1	2	3	4	1	2	3	4
S_m; *Calanus* . . .	3310	3420	3530	3630	3710	3770	3770	3600
S_m; 'other copepods' . .	70	70	70	70	70	70	70	70
	March				*April*			
	1	2	3	4	1	2	3	4
S_m; *Calanus* . . .	2000	920	710	640	600	600	660	900
S_m; 'other copepods' . .	70	70	70	70	70	70	70	70
	May				*June*			
	1	2	3	4	1	2	3	4
S_m; *Calanus* . . .	1160	1270	1270	1190	1050	900	730	560
S_m; 'other copepods' . .	70	70	70	70	70	70	70	70

two values are expressed as mls/day and are added. The sum is expressed as a fraction of 1 litre to give the weekly value of G, the grazing rate; this is because the model is worked in units of volume of 1 litre.

I (iii) THE REPRODUCTION OF HERBIVORES

The herbivore populations are considered as two groups: *Calanus* and 'other copepods'. 'Other copepods' include the genera *Temora*, *Pseudocalanus*, *Paracalanus*, *Microcalanus*, *Acartia*, *Oithona* and *Centropages*. From Wimpenny's observations on the Flamborough Line from January to June, 1947–50, the percentages of *Calanus* were as given in Table VI; weekly estimates were interpolated from a series of mean monthly values.

TABLE VI

Percentages of Calanus *in the herbivore population, by weeks between January and June*

Months:	January				February				March				April			
Weeks:	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
%	20	19	19	18	18	17	16	17	18	20	22	24	26	28	26	22
Months-					May				June							
Weeks:					1	2	3	4	1	2	3	4				
%					18	14	10	9	8	7	6	5				

Before the reproduction of the herbivore population is considered, the proportion of females must be established. In late winter, the proportion of females in the *Calanus* population is high because they are the mature individuals of the overwintering group. The proportion is not so high in the 'other copepod' population. Table VII gives the percentage of female *Calanus* by weeks from Wimpenny's observations on the Flamborough Line and the percentage of females in the 'other copepod' population taken from Digby (1950) and from Marshall (1949); Digby used a silk of 120 meshes to the linear inch and Marshall used one of 200 meshes to the linear inch, so it is unlikely that any of the smaller individuals escaped capture.

TABLE VII

Percentages of females in Calanus *and* 'other copepod' *populations by weeks from January to June*

Months:	January				February				March			
Weeks . . .	1	2	3	4	1	2	3	4	1	2	3	4
Calanus . . .	20	30	42	55	65	70	70	66	58	48	38	29
'other copepods' .	30	26	23	21	20	19	19	20	21	21	21	19
Months:	April				May				June			
Weeks . . .	1	2	3	4	1	2	3	4	1	2	3	4
Calanus . . .	20	13	9	6	5	5	6	8	11	15	20	24
'other copepods' .	16	14	13	13	13	14	15	16	17	19	21	22

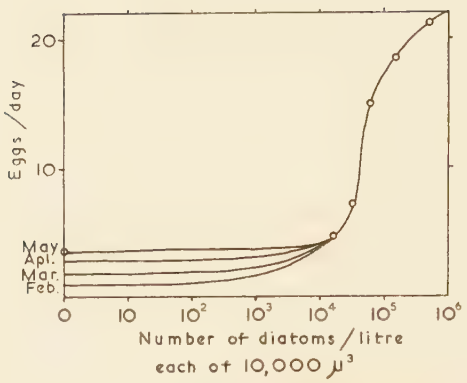

FIG. 8. *Egg production of* Calanus *in eggs/day as a function of diatom concentration (from the data of Marshall and Orr*, 1952).

We consider reproduction in two parts, firstly the production of the eggs and, secondly, the survival of eggs to the commonest copepodite stage, which is stage III or IV (these are the most numerous, because they are the first of the long-lived stages).

A detailed study of egg production in *Calanus* has been made by Marshall and Orr (1952). Their most important finding was a relation between the numbers of eggs/*Calanus*/day and the number of cells of *Chlamydomonas* in the culture medium. When starved, the animals produced from 0·8 to 2·8 eggs/day, whereas in a culture of 70–250 cells/mm^3, they produced 20 eggs/day. Figure (8) shows the results of this work converted to numbers of algal cells of 10,000 μ^3 in size (assuming that the volume of a single *Chlamydomonas* cell was 20μ^3).

Figure (8) also gives some estimates of egg production by starved animals. Marshall and Orr give a considerable quantity of data on this point (their text figure (2), their text on p.536 and their Tables V, VI, and VII); it shows mainly that the 'Starved' level of egg production in eggs/*Calanus*/day increases during the spring:—

January	*February*	*March*	*April*	*May*
0·9	0·9	1·8	2·8	3·6

Weekly values of eggs/*Calanus*/day were interpolated as follows:—

Months:	January				February				March			
Week . . .	1	2	3	4	1	2	3	4	1	2	3	4
Eggs/*Calanus*/day .	0·9	0·9	0·9	0·9	0·9	0·9	0·96	1·14	1·39	1·66	1·94	2·20

Months:	April				May			
Week . . .	1	2	3	4	1	2	3	4
Eggs/*Calanus*/day .	2·45	2·69	2·92	3·14	3·34	3·52	3·67	3·80

Thus, with the use of Figure 8 it is possible to estimate the egg production at any time and at any level of algal numbers. Marshall and Orr's results were worked out for *Calanus* only; it is likely, however, from Marshall (1949) that a similar relation holds for '*other copepods*'. In 1933, the diatom outburst took place during March and April and there was a second outburst in June; the number of eggs/egg-sac for *Pseudocalanus minutus* in February was 9·5 and in April it was 37·1. Similarly, the number of eggs/egg-sac for *Oithona similis* was 5·6 in January, 16·8 in March and 18·4 in June.

The second stage in reproduction is the survival of the juveniles. From a Scottish loch, Nicholls (1933) has published detailed analyses of catches of eggs, nauplius stages and copepodite stages of *Calanus*; the relevant results are given in Table VIII.

TABLE VIII

Numbers of Calanus *of all stages caught by a Fine net*

	Ova	*Naupliar stages*						*Copepodite stages*						
		1	2	3	4	5	6	I	II	III	IV	V	♂	♀
7.III.32	119	4	4	4	5	1	3	11	1	–	–	–	–	–
21.III.32	117	10	9	11	4	4	5	20	36	35	13	2	–	–
5.IV.32	13	3	1	–	1	–	–	–	14	75	87	55	6	7

Marshall and Orr (1954) have shown that the eggs hatch in 24 hours and so the figures in March represent an egg production of about 120 eggs/day/unit volume of water. From Nicholls' (1933) experimental determinations of the duration of copepodite stages, it is likely that the minimum time to reach copepodite stage II is 15 days; thus the copepodites alive on 5th April were probably hatched between 7th and 21st March. Consequently 1,560 eggs gave rise to 244 copepodite stages, a mortality of 80%. The egg number may have been higher before the 7th March, but that is unlikely, because the diatom outburst in Loch Striven started at just about that date (Marshall and Orr, 1934). Similar analyses lead to estimates of mortality of 93% for a period of about 15 days centred on 9th May and of 92% centred on 15th May. Table IX sets out the estimated % mortalities from January to June by weeks; each percentage represents the reduction from the number of eggs to the number of copepodite stage IV's at the mid-point between the date of egg laying and the date of appearance of the stage IV's.

TABLE IX

Estimated percentage mortality for juvenile Calanus *in weekly periods*

Months:	February				March				April			
Weeks . . .	1	2	3	4	1	2	3	4	1	2	3	4
% . . .	80	80	80	80	80	80	83	86	87	90	93	97

Months:	May				June			
Week . . .	1	2	3	4	1	2	3	4
% . . .	97	97	97	97	97	97	97	97

The larger copepodite stages (IV–VI) live longer, the females much longer than the males. There is no information about the mortality of these stages and so it has been set arbitrarily as a duration of life of eight weeks. This means that the copepodites are added to the stock on attaining to stage IV and the same number is subtracted eight weeks later.

Summarising, there are three stages in the life of the idealized herbivores used in the model, firstly, egg production, secondly, juvenile mortality and lastly adult mortality.

I (iv) ON THE INITIAL NUMBERS OF ALGAE AND HERBIVORES

There are only four observations published of the numbers of diatoms in winter in a region reasonably close to the North Sea. Counts of diatoms are given in Table X.

Three sets of observations were taken in coastal water and one in the Norwegian Sea; a reasonable estimate would be 100 to 1,000 cells/litre, which is rather similar to an observa-

TABLE X

Numbers of diatoms/litre in winter in the region adjoining the Northern North Sea

Oslofjord	*Kiel Bay*	*Isefjord*	*Weather Ship 'M'*
850	253	250	500
1150	323		120
			160
(Gaarder and Gran, 1927)	(Lohmann, 1908)	(Steemann Nielsen, 1951)	(Sverdrup, 1953)

tion in the Gulf of Maine made by Bigelow, Lillick and Sears (1940)—1,760 cells/litre. In all cases many of the species recorded were small in size and so a reasonable value for cells of 10,000 μ^3 would be 0·1 to 100 cells/litre. In fact an initial value of 1·25 cells/litre was used in the model.

For the numbers of herbivores, Wimpenny's observations from the Flamborough Line were used. Table XI gives the actual numbers of zooplankton in winter, which is predominantly composed of herbivorous copepods.

TABLE XI

Numbers of Zooplankton per cubic metre on the Flamborough Line

	1935	1936	1937	1938	1939	1947	1948	1949
January . .	80	18	71	188	53	74	144	64
February . .	35	52	32	206	56	185	40	50

From 96 observations, the mean number of herbivorous zooplankton, excluding nauplii, was 84·3/m^3 or about 0·1/litre. In Kiel Bay, Lohmann (1908) found 35 herbivores/litre in winter; between Iceland and Faroe, Hentschel (1936) found 200 to 500 herbivores/m^3, or 0·2 to 0·5/litre; off Plymouth, Harvey *et al* (1935) found 4160/m^3 or 4·2/litre and Digby (1950) found 0·6/litre of 'other copepods'. There is considerable variation between the different regions, so Wimpenny's observations have been used because they were made in the central North Sea and they are consistent from year to year.

A further analysis of Wimpenny's results for the period 1935–1949 (excluding the war years), shows that the average number of *Calanus* copepodite stages (including stage VI) in January was 0·01/litre and that the corresponding figure for 'other copepods' was 0·07/litre. These figures were used as the initial numbers for the two groups of herbivores in the operation of the model.

Summarizing, for entering in the model, the initial numbers of algae and herbivores will be:—

Algae of 10,000 μ^3	*Calanus*	*'other copepods'*
1·25/litre	0·01/litre	0·07/litre

I (v) THE OPERATION OF THE MODEL

The model is basically a single algal population which is being grazed by two herbivore populations, the grazing activities of which are added. The reproductive activities of the two herbivore populations are kept separate. Formally, the model is expressed as follows:—

$$\frac{dP}{dt} = (R - G)P \quad . \quad . \quad . \quad . \quad . \quad . \quad 1$$

$$\frac{dH}{dt} = (R_H - M_H)H \quad . \quad . \quad . \quad . \quad . \quad 2$$

where P is the number of algae per litre;
R is the daily instantaneous algal reproductive rate;
G is the daily instantaneous rate of grazing mortality of the algae;
H is the number of herbivores per litre;
R_H is the daily instantaneous reproductive rate of the herbivores;
M_H is the daily instantaneous mortality rate of the herbivores;
t is time.

In this formulation herbivores are grouped as one population, for simplicity; in the model, two groups are used, *Calanus* and 'other copepods'.

Equations 1 and 2 are linked in the following way:—

$$G = f(H) \quad . \quad . \quad . \quad . \quad . \quad . \quad 3$$

$$R_H = f(P) \quad . \quad . \quad . \quad . \quad . \quad . \quad 4$$

Of the other parameters, R, the algal reproductive rate, is dependent upon the sun and the wind, and M_H, the herbivore mortality rate, is set at an arbitrary value compatible with certain field observations.

So far we have been concerned with estimating R, G, R_H and M_H and with establishing initial numbers for P and H. The model is run in weekly stages and is started in the third week of February. This is because the critical depth is too great until then, in the water of about 40 fm, north of the Dogger Bank; the critical depth is defined as follows (Sverdrup, 1953):—

$$D_{cr} = \frac{D_c . e^{k.Dc}}{k.D_c}$$

where D_c is the compensation depth;
k is the extinction coefficient;
D_{cr} is the critical depth;
when $D_{cr} > D_m$, the depth of mixing, the energy of photosynthesis is used entirely in respiration, because the algae spend insufficient time in the euphotic zone. The critical depth is defined as the depth at which the total photosynthesis in the water column is equal to the total respiration; it is about five to nine times greater than the compensation depth, at which the rates of photosynthesis and respiration are equal.

An example of the operation of the model is shown in two tables:—

TABLE XII

An example of the operation of the model

A. Calanus

	A	*B*	*C*	*D*	*E*	*F*
	% ♀	% *survival*	*Eggs/* ♀*/day*	*Eggs/week*	*Copepodites produced*	*Copepodites in stock*
Jan. 1	20	20	0·90	0·013		
2	30	20	0·90	0·019		
3	42	20	0·90	0·026		
4	55	20	0·90	0·035		
Feb. 1	65	20	0·90	0·052	0·0026	0·0126
2	70	20	0·90	0·072	0·0038	0·0164
3	70	20	0·96	0·102	0·0052	0·0216
4	66	20	1·14	0·151	0·0070	0·0286

B. 'other copepods' is very similar to Table A.

C. *Algal numbers*

	R	*G*	*R-G*	*(R-G)T*	$e^{(R-G)T}$	*P*	$P.e^{(R-G)T}$
Jan. 1						1·25	
2						1·25	
3						1·25	
4						1·25	
Feb. 1						1·25	
2						1·25	
3	0·160	0·101	0·059	0·413	1·511	1·25	1·889
4	0·192	0·128	0·064	0·448	1·565	1·889	2·956

T is seven days.

The model starts in the first week of January with 0·01 *Calanus*/litre; the number of eggs/♀/day is 0·90 (Col. C); the number of eggs/week is $0{\cdot}01 \times 0{\cdot}90 \times 0{\cdot}20 \times 7 = 0{\cdot}013$ (Col. D); the survivors as copepodites are produced four weeks later, $0{\cdot}013 \times 0{\cdot}20 = 0{\cdot}0026$ (Col. E); this value is added to the stock, $0{\cdot}010 + 0{\cdot}0026 = 0.0126$ (Col. F).

The model is then operated in this way until the third week of February, when the algal numbers increase. The algal reproductive rate, *R*, is calculated as shown in an earlier section. The grazing rate, *G*, is estimated from the methods given above. For example, at an algal density of 1·25 cells/litre in the third week of February, S_0, the volume swept clear, for *Calanus*, is 3,770 mls/day; the number of *Calanus* is 0·0216/litre, so the volume swept clear is $3{,}770 \times 0{\cdot}0216$ mls/day = 81; the analogous value for 'other copepods' is 20 mls, so the total for the two herbivore populations is 101/mls/day. As the unit of volume is 1,000 mls, the grazing rate is 0·101. The initial value of *P* is then raised by $e^{(0.160-0.101)7} = 1{\cdot}511$ to give the value of P for the fourth week of February.

There are two other operational details. The first is that the number of eggs/♀/day is determined by the value of *P* in any week, as shown in the relation in Fig. 8. The other point is that the increment of copepodites to the adult stock is subtracted eight weeks later, representing an average mortality of older copepodites.

The results of the calculation are shown in Fig. 9; there are the following points to be noticed:—

(1) the curve of algal production is symmetrical and bell shaped (Fleming 1939);
(2) the algal production reaches its peak in the last week in April;
(3) the peak of the algal standing stock is $0{\cdot}56{\cdot}10^9$ μ^3/litre;
(4) the weight of *Calanus* increases quickly until the last week of April, after which it increases less quickly; in numbers, *Calanus* reach about 0·50/litre.
(5) The weight of 'other copepods' increases steadily from January to June; in numbers, 'other copepods' reach 4·0/litre.

From the observations on the Flamborough Line, the average peak numbers of *Calanus* were 0·40/litre and for 'other copepods' were 2·2/litre. The only observation on algal abundance was made in 1949 off the north-east coast of England (Cushing, 1955) and was $0.5.10^9$ μ^3/litre. The algal peak occurs towards the end of April, the *Calanus* peak in May and the 'other copepods' peak in June.

Figure (9) shows that algal numbers after the peak decline at the rate of ten times in a fortnight. Cushing (1955) found a rate of decline of algal numbers in the sea of six times in three weeks. The somewhat excessive rate of decline in the model is probably associated with the excess production of *Calanus* and 'other copepods', particularly after the peak of algal production. It is unlikely that the adult mortality of herbivores is constant and it should probably be increased when the herring aggregate. At the moment the extent of this mortality is unknown, although Cushing (1955) produced evidence that it is high.

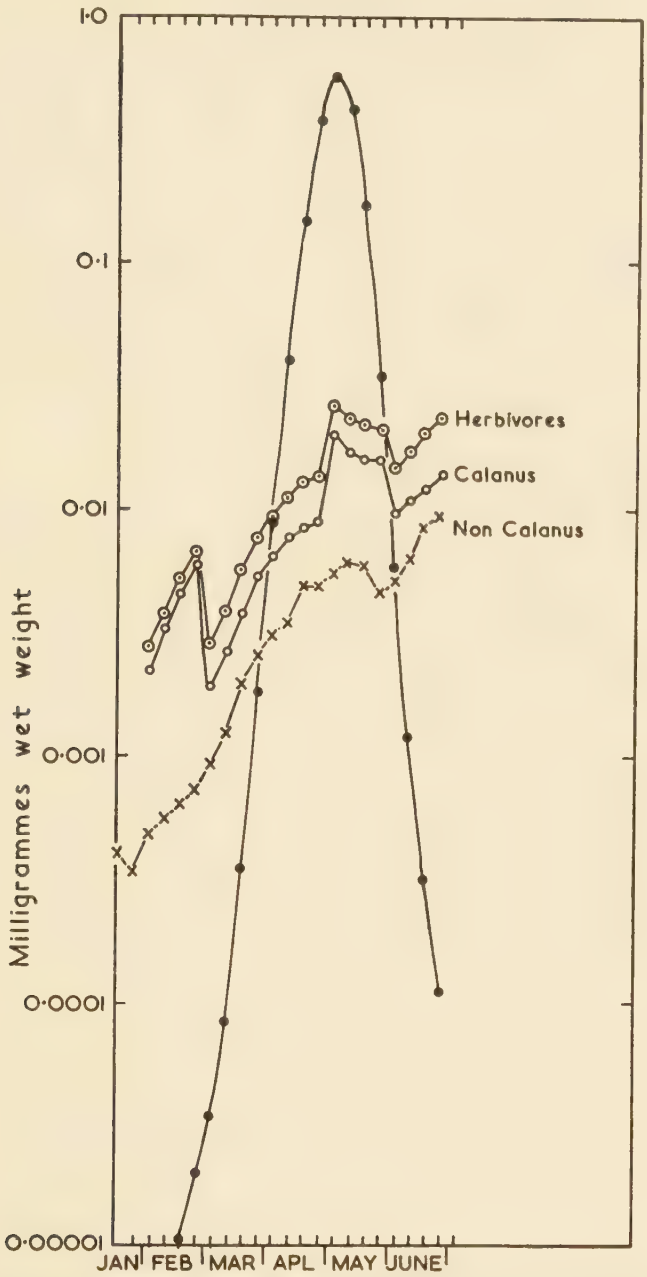

FIG. 9. *The theoretical production of algae,* Calanus *and 'other copepods' as mg wet weight/litre from January to June.*

Production may be calculated in the weekly periods and summed for the whole period, T, using the following formulae:—

$$\frac{PR}{R - G}\,(e^{(R-GT} - 1),$$

for the algal population, and,

$$\frac{H.R_H}{R_H - M_H}\,(e^{(R_H - M_H)T} - 1),$$

for the herbivore populations; where T is one week the algal production is computed quite readily from the values in Table XII. For the calculation of herbivore production certain additional estimates are needed:

(1) total mortality is taken from Table XII in each week, and is divided by 7 to give M_H.

(2) H, the number of herbivores is divided by the increment of copepodites in each week to give $(R_H - M_H)T$.

(3) knowing M_H and $(R_H - M_H)T$, we can obtain R_H.

Weights of production were calculated using the following equivalents:—

(1) 1 mg wet weight of algae $= 10^9\ \mu^3$.

(2) 1 *Calanus* V weighs 0·53 mg wet weight (Bogorov, 1934); for other sizes a correction by the cube of the length was used.

(3) 1 'other copepod' weighs 0·01 mg wet weight.

(4) Wet weight: dry weight ratio is 9: 1 for zooplankton and 5: 1 for phytoplankton. (Sverdrup *et al.* 1942).

(5) 1 g dry weight = 0·44 gC (Sverdrup *et al.* 1942).

(6) depth of water column is 70 m.

For the whole period of six months, the quantities of production are given in Table XIII.

TABLE XIII

Quantities of production from January to June

	Per unit volume mg/l wet weight	*Beneath unit surface* g.C/m²	*Average daily rate* g.C/m²/*daily*
Algal production (P_R) . . .	1·78*	6·08	0·034
Quantity of algae grazed (P_G) .	1·78*	6·11	0·034
Calanus production ($P_H{}^1$) . .	0·179	0·61	0·0034
'Other copepod' production ($P_H{}^2$).	0·077	0·264	0·0015

*Note: These values are the same because the final value of algal standing stock is very small compared with the total production.

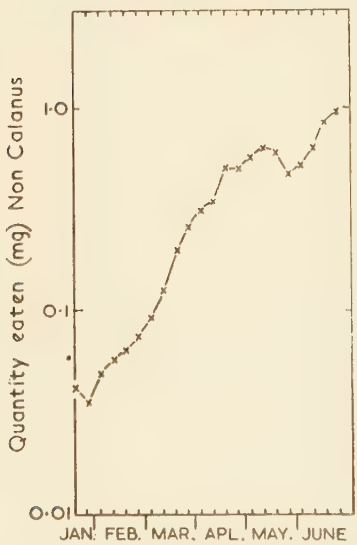

FIG. 10. *The theoretical quantity eaten by 'other copepods' in mg wet weight/litre.*

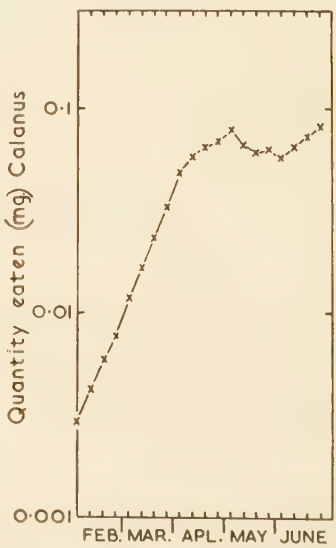

FIG. 11. *The theoretical quantity eaten by* Calanus *in mg wet weight/litre.*

Figures (10), (11) and (12) show the algal production and quantity grazed (Figure (12), and the quantity eaten by *Calanus* (Figure 11) and by 'other copepods' (Figure 10). The total herbivore production is one seventh of the algal production and 2/9 of the quantity of algae eaten by the herbivores. Figure (13) shows the course of the ratio $P_G/P_H{}^1 + P_H{}^2$ and it will be seen that the season starts and ends with the herbivores apparently under-nourished, but at the height of the production season they appear to feed to excess. During the high season, there is thus some overproduction which is lost to the immediate productive system and probably feeds the benthos. Thus, we have returned to the idea of Harvey, Cooper, Lebour and Russell (1935) that grazing produces more material as faecal pellets than the herbivores immediately require.

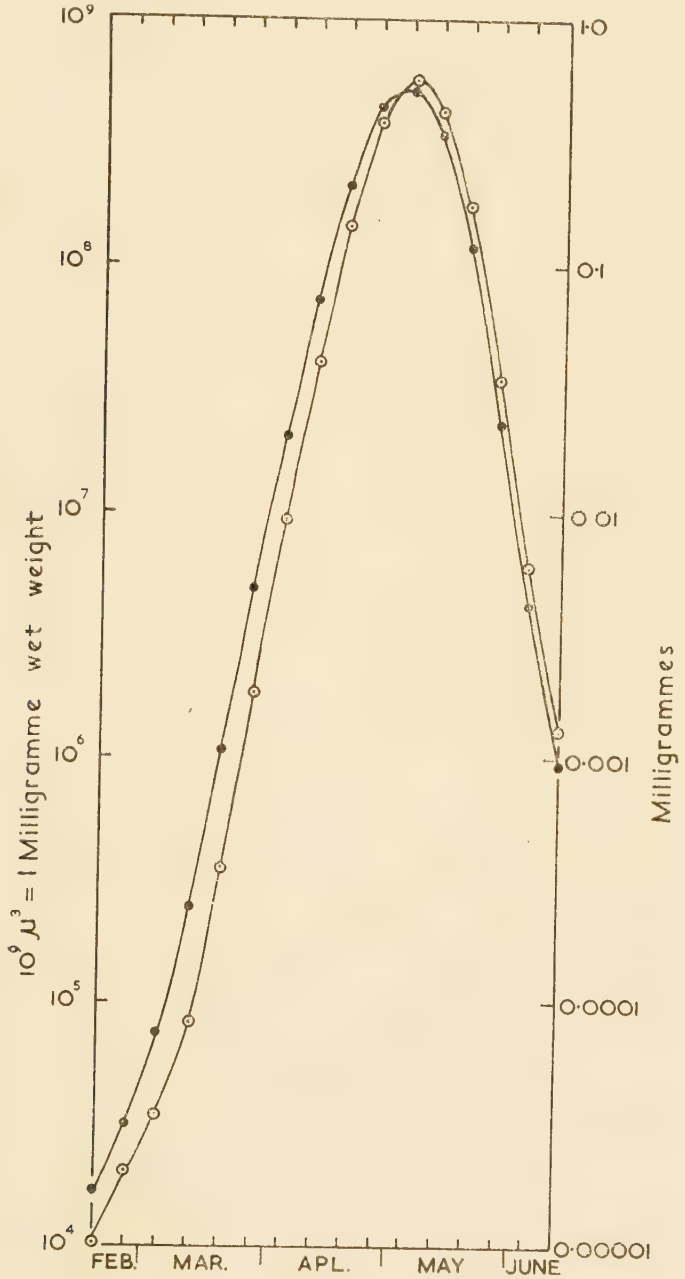

FIG. 12. *The theoretical curve of algal production* (●——●) *with the quantity of algae eaten* (○——○).

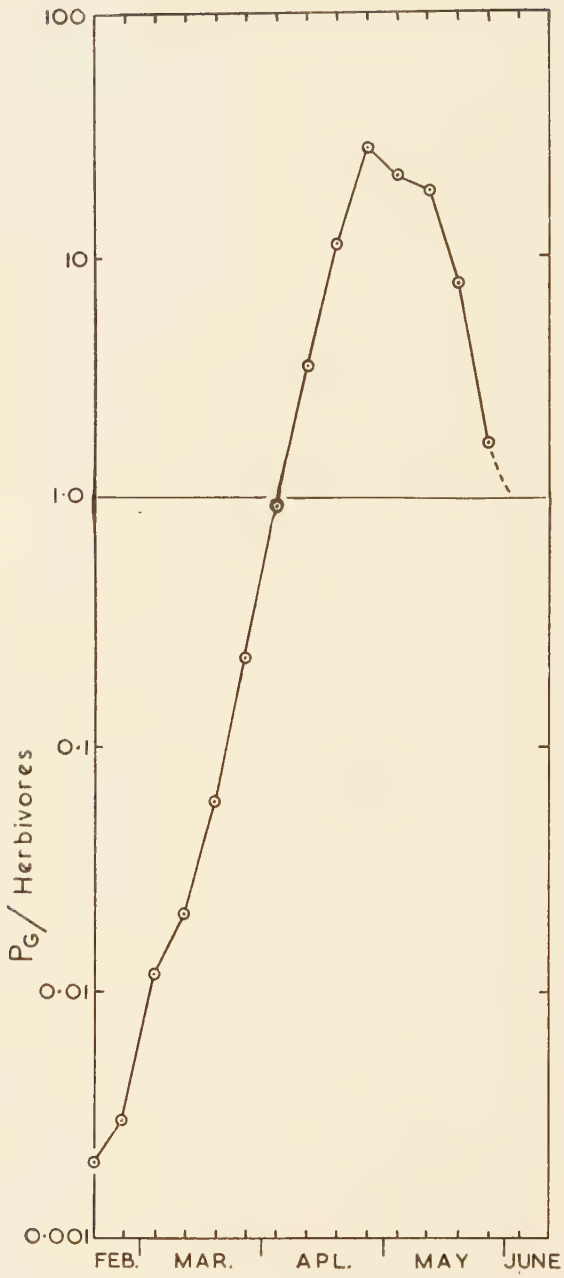

FIG. 13. *The ratio of quantity grazed to the weight of herbivores.*

Lastly, it should be pointed out that the model is restricted to the spring or early summer production in temperate seas, to the 'spring outburst' proper.

II. THE BALANCE OF NUTRIENTS IN THE WATER

II (i) INTRODUCTION

The simplest model of a productive system is an algal culture grown under constant environmental conditions with varied quantities of added nutrient. Using a culture of *Nitszchia closterium*, Atkins (1925) showed that as the quantity of diatoms increased so the phosphorus content of the culture medium declined. Again, Harvey (1933) and Spencer (1954) have demonstrated in culture a linear relation between the quantity of nutrient added and the quantity of crop produced. This relation was the basis of the *Chlorella* project (Burlew, 1953), in which a steady state system was set up between added nutrients on the one hand and produced crop on the other. However, it has been shown that the cell content during the spring outburst in Windermere declines (Mackereth, 1953) and that the change in cell content of phosphorus is proportional to the change in the algal standing stock. His Figure (7) shows a clear correlation between cell number in Windermere and the ratio of cell silica to cell phosphorus. As the cell silica is constant, this means that the change in cell content of phosphorus is proportional to the change in algal standing stock.

The change in cell content of phosphorus shown by Mackereth implies that the productive system is more complex than assumed in the culture experiments. If the cell phosphorus was shared out amongst all the produced cells, then it would decrease far more quickly than inversely as the rate of increase of the standing stock.

If it is supposed that phosphorus is truly distributed in all the produced cells, then the balance must be made up from somewhere; the simplest hypothesis is to assume that much nutrient is immediately returned to the water in the act of grazing. This accounts for the decrease in cell content being proportional to the standing stock and not to the production.

Gardiner (1937) kept plankton animals in sea water for short periods and found that the increase in phosphorus in the culture flasks due to excretion amounted to 0·068 μg *P*/animal/day. I have carried out a similar experiment in the North Sea using *Calanus* V and have found a phosphorus excretion rate of 0·35 μg *P*/animal/day; the difference between the two estimates is probably because I used larger animals during the spring outburst, when grazing might have been excessive. From the weight of *Calanus* and the C : N : P proportions in living tissue the expected excretion would have been 0·05 μg *P*/animal/day. Excessive grazing was shown to be a distinct possibility in the earlier sections of the present paper; one of the consequences of excess grazing would be that immediate regeneration of nutrients to a sizeable proportion became a real possibility. The apparent decline in phosphorus off Plymouth in 1931 was about 0·9 μg/*P*/litre/week; the numbers of *Calanus* in the North Sea at the period of the spring outburst are 0·1 to 0·3/litre. If they excreted at 0·35 μg/day, a high but observed value, the total excretion would be 0·25 to 0·75 μg *P*/litre/week; if they excreted at 0·07 μg/day, a value nearer the expected value, the total excretion would be 0·05 to 0·25 μg *P*/litre/week. As the 'other copepods' have been neglected, it appears that immediate regeneration must have a significant effect.

It is possible that the regeneration of silica may be best accounted for on the basis of grazing. Diatom frustules do not dissolve readily in sea water and Cooper (1952) has suggested that they can only be dissolved after fracture by grazing. Holt and King (1955) have shown that the solubility of silica is inhibited by an adsorbed monolayer of silicic acid, so the only time for solution is the short period between fracture and the re-formation of the monolayer. It is possible that silica can only dissolve in the sea after being fractured by grazing; if this is really so, then grazing mortality must be nearly complete, to allow for silica replenishment.

In the next section it is assumed that uptake of nutrient is proportional to production and that its immediate regeneration is proportional to grazing; the consequences of these assumptions are explored.

II (ii) THEORETICAL MODEL OF THE UPTAKE OF ALGAL NUTRIENTS IN WATER

Let us suppose that the uptake of nutrient from the water by the algae is directly proportional to algal production, i.e.,

$$U_n = N_c \,.\, P_R \,, \qquad . \quad . \quad . \quad . \quad . \quad . \quad 1$$

where U_n is the uptake of nutrient, N, in μg/litre between time t_0 and time t_1,
N_c is the quantity of nutrient/cell in μg,
P_R is the quantity of algae produced per litre between time t_0 and t_1.

Let us suppose that the regeneration of nutrient to the water is proportional to the quantity of algae grazed, i.e.,

$$R_n = N_c \,.\, P_G \qquad . \quad . \quad . \quad . \quad . \quad . \quad 2$$

where R_n is the regeneration of nutrient, N, in μg/litre between time t_0 and time t_1,
P_G is the quantity of algae grazed per litre between time t_0 and t_1.

$$P_R = \frac{P \,.\, R}{R - G} \cdot (e^{(R-G)(t_1 - t_0)} - 1) \qquad . \quad . \quad . \quad . \quad . \quad 3$$

and

$$P_G = \frac{P \,.\, G}{R - G} \quad (e^{(R-G)(t_1 - t_0)} - 1) \qquad . \quad . \quad . \quad . \quad . \quad 4$$

The balance between uptake and regeneration is expressed by

$$N_c(P_R - P_G) = N_c(P_1 - P_0) = -\,N_c(P_0 - P_1), \qquad . \quad . \quad . \quad 5$$

where P_0 and P_1 are numbers of algae, P, at time t_0 and t_1.

This is only an incomplete balance, because nutrients are also taken up into animals by grazing and are also lost to the productive system as faecal pellets. This loss may be estimated by bringing in the decrement of nutrient in the water, $N_0 - N_1$, from time t_0 to time t_1. The simplest nutrient is silica which is not used by most animals and probably appears only in some algae and faecal pellets. The loss of nutrient, L, to the productive system may be expressed as follows:—

$$L = N_0 - N_1 - N_c(P_R - P_G) = N_0 - N_1 + N_c(P_0 - P_1) \qquad . \quad . \quad 6$$

If there were no loss and N_c were constant, $N_c = \dfrac{N_0 - N_1}{P_1 - P_0}$,

$P_1 - P_0$ being expressed as weight of silica. When P_G is small and few faecal pellets are produced, the reduction of silica is proportional to the increase in the algal standing stock. When P_G is large, the reduction of silica is the quantity taken up in the change of standing stock added to the quantity lost as faecal pellets.

When a nutrient is also used by animals, for example, phosphorus, then $R_n \neq N_c \,.\, P_G$, because some phosphorus remains in organic form during the time period $t_1 - t_0$.

Let $$R_n = N_c P_G \,.\, a, \qquad . \quad . \quad . \quad . \quad . \quad . \quad 7$$

where a is the fraction of nutrient immediately excreted and so $(1 - a)$ is the fraction remaining in organic form.

Then $$L = N_0 - N_1 - N_c(P_1 - P_0) + N_c P_G(1 - a) \qquad . \quad . \quad . \quad 8$$

It is characteristic of the use of phosphorus that the quantity of nutrient per cell is inversely related to the quantity in the standing stock (Mackereth 1953), i.e.,

$$ {}_0N_c \,.\, P_0 - {}_1N_c \,.\, P_1 = 0 \quad . \quad . \quad . \quad . \quad . \quad . \quad 9 $$

where ${}_0N_c$ is the quantity of nutrient/cell at time t_0 and ${}_1N_c$ is the quantity at time t_1. Consequently Eqn. 8 can be more exactly formulated as,

$$ L = N_0 - N_1 - \overline{{}_0N_c \,.\, {}_1N_c}(P_1 - P_0) + \overline{{}_0N_c \,.\, {}_1N_c} \,.\, P_G(1 - a) \quad . \quad . \quad 10 $$

where $\overline{{}_0N_c \,.\, {}_1N_c}$ is an average value, expressing the change in quantity over the period $t_1 - t_0$.

In other words, L, the loss of phosphorus from the productive system, is proportional to the quantity of nutrient released from the algae by grazing, into a living animal form or a dead organic form.

Considering the limiting effect of nutrients, there are two possible assumptions which are formally the same:—

(a) from $0 - x$ μg/litre, $R \propto \dfrac{1}{N}$,

where R is the daily instantaneous reproductive rate of the algae; in other words, the algal reproductive rate is inversely proportional to the nutrient content of the water;

(b) when $N = 0$ μg/litre, $U_N = 0 \quad \therefore N_c P_r = 0.$

Let us assume that at time $T > t_0$, $< t_1$ at which $N_T = 0$, production stops because the algal reproductive rate is nil. Consequently, after time T, $R - G$ becomes negative, so T is the time of maximum standing stock.

When N_c is constant, at time T, $N_c(P_T - P_0) = N_0 - L_T \quad . \quad . \quad . \quad . \quad . \quad 11$

where L_T is the loss of nutrient from the productive system, between t_0 and T.

The next thing that happens is that the standing stock is reduced by grazing and of course more nutrient becomes available for production and so production can continue. Such a limit would be difficult to discern; in fact the only way in which it could be done would be to show that the algal reproductive rate had been reduced at the time of peak algal standing stock.

II (iii) THE LOSS OF NUTRIENT FROM THE PRODUCTIVE SYSTEM

Lund (1950) has made a very detailed study of the production of *Asterionella formosa* Hass in Windermere, which has already been used in Figure (1). The diatoms were counted once a week from the top 5 m of the lake; at the same time, estimates of weekly division rates were made from diatom counts in culture flasks suspended at 0·5 m, 5 m, and 7 m. Determinations of the silica content of the water were also made each week. The estimates of division rate in the culture flasks were free of any possible effects of nutrient depletion or of turbulence. In the lake, the peak of algal numbers was reached in the last week of May; as the thermocline developed in the second week of May (Mortimer, 1952), it is unlikely that division rates in the lake were reduced by turbulence to any great extent; again, during the last three weeks of May, the silica content of the euphotic zone was high, so it is unlikely that division rates were much reduced by silica depletion. Table XIV gives a calculation of the loss of silica to the productive system.

TABLE XIV

The loss of silica from the productive system in Windermere, 1947

Week	*Month*	P *cells/ml*	*Light K.lux hrs*	N *mg/l*	R	R-G	*Loss mg/l*
1	May	240	500	2·2			
					8·6	0·88	0·11
2	May	900	880	2·1			
					8·5	1·31	0·10
3	May	2,500	850	1·8			
					11·5	0·96	− 0·21
4	May	4,000	500	1·8			
					9·5	0·56	0·36
5	May	5,000	460	1·3			
					8·8	0·18	0·85
1	June	2,500	620	0·8			
					7·5	− 0·69	0·50
2	June	1,100	600	0·5			
					10·5	− 0·82	0·12
3	June	280	480	0·5			
							1·83

Note: $R - G = \frac{1}{t} . \log_e \frac{P_1}{P_0}$, where t is one week.

Let $N_c = 0{\cdot}14 . 10^{-6}$ mg SiO_2 (Lund 1950);
Let P_1 be $5{\cdot}10^6$ cells/litre, the maximum value of standing stock;
Let P_0 be 1 cell/litre
Then $N_c(P_1 - P_0) = 0{\cdot}70$ mg SiO_2/litre
then the silica budget is:—

Loss 1·86 mg/Litre SiO_2

$N_0 (P_1 - P_0)$ 0·70 mg/Litre SiO_2
2·56 mg/Litre SiO_2

There is some doubt whether *Asterionella* is actually consumed by herbivores, in which case there is a high mortality rate, here named the grazing rate, due to some other causes, perhaps fungal parasitism (Canter and Lund, 1951). But, from the figures, it is likely that the total quantity of silica passed through the system a number of times, which implies that rapid regeneration occurred, whatever the cause of mortality.

The highest observed quantity of silica in the water in the winter of 1946–7 was 2·50 mg/litre SiO_2. Thus the total use of silica is accounted for. It is worth pointing out that the loss of silica from the productive system was greatest between the fifth week of May and the second week of June. This is the period of declining algal numbers, when grazing is most intense; in fact the total loss during this period (1·35 mg SiO_2) is nearly twice that in the peak algal standing stock (0·70 mg SiO_2).

Lund (1950) has published a long series of observations relating the winter maximum of silica to the peak standing stock of *Asterionella* in the ensuing summer. When plotted against each other, the points are randomly scattered. This must mean that in any given year, the loss was a considerable proportion of the use of nutrient and that this proportion varied from year to year. In the example given above, the loss is greater than the quantity in the standing stock.

From the data given in Table XIV, we may also calculate the production week by week, using the formula

$$\frac{P . R}{R - G}(e^{(R-G)t} - 1),$$

where t is one week. Using the value of $N_c = 0{\cdot}14 . 10^{-6}$ mg SiO_2, the total quantity of silica used in the productive processes during the spring outburst may be calculated. It

amounts to 17·5 mg SiO_2/litre, or seven times the winter maximum, up till the fifth week of May; therefore, the total silica budget was turned over seven times before the greatest period of loss started.

When the winter maximum of phosphorus is considered as an index of fertility, it must be realized that the total algal production is not being indicated. Using Lund's results and a value of cell content making a calculation analogous to that for silica, it is possible to show that phosphorus was used over and over again more than thirty times. Now the loss of silica is presumably mainly in faecal pellets, but the loss of phosphorus is mainly in animal flesh. Thus the winter maximum of silica indicates something like the maximum standing stock of algae, whereas the winter maximum of phosphorus mainly indicates the quantity of herbivores produced. This accounts for the silica/phosphorus anomaly observed by Atkins (1926) and Cooper (1933), when the quantity of production from the decline in phosphorus was seven times that from the decline in silica in the English Channel. This could mean that the quantity of herbivores produced was seven times greater than the maximum algal standing stock and faecal pellets. The two estimates probably deal with different parts of the productive system.

It appears that the winter maximum of phosphorus, less a quantity locked in the previous summer's production, indicates the quantity of herbivores that will be produced. Because the residue from the previous year's production can obviously vary, the index of future fertility is also variable. This is an exact parallel with the winter maximum of Windermere, which did not indicate the magnitude of algal standing stock, because the loss of silica was unpredictable; the winter maximum of phosphorus does not indicate the magnitude of herbivore production, because the loss of phosphorus (in the perennial herbivore stock, as opposed to the annual herbivore stock) is also unpredictable.

II (iv) THE EFFECT OF GRAZING AS COMPARED WITH THE EFFECT OF NUTRIENTS

A nutrient limit to production (as opposed to a reduction in algal division rate at low nutrient levels) can be detected only by observations at the time of peak standing stock. In order to demonstrate such a limit, observations on standing stock and nutrient cell content are necessary at frequent intervals. After production has been slowed or halted, grazing continues and more nutrient becomes available. Thus, during the spring outburst, the way in which nutrients limit production can at best be transitory and therefore difficult to demonstrate precisely, if indeed it really occurs.

There is, however, usually a decline in nutrients that runs parallel to the course and timing of production. The decline is most marked when the algal numbers are decreasing and when grazing is most intense (see Table XIV). If the loss from the productive system were proportional to production, nutrients would decline during the whole course of production.

Let $$L = m \,.\, N_c \,.\, P_R,$$

where m is a constant fraction.

For silica, $L = N_0 - N_1 - N_c(P_1 - P_0)$

$$N_0 - N_1 = m \,.\, N_c \,.\, P_R + N_c \,.\, P_R - N_c \,.\, P_G$$

$$= \frac{m \,.\, N_c \,.\, P_0 \,.\, R}{R - G}\,(e^{(R\ \ G)t} - 1) + \frac{N_c \,.\, P_0 R}{R - G}\,(e^{(R\ \ G)t} - 1)$$

$$- \frac{N_c \,.\, P_0 \,.\, G}{R - G}\,(e^{(R-G)t} - 1)$$

$$= \frac{N_c \,.\, P_0\,(e^{(R\ \ G)t} \quad 1)}{R - G}\,(m \,.\, R + R - G)$$

$$\frac{N_c(P_1 - P_0)}{R \quad G}\,(R\,(m + 1) \quad G)$$

The nutrient decline is described by the fraction $\frac{R(m+1)-G}{R-G}$

It has been shown above that the total silica 2·5 mg SiO_2/l was used about seven times during the productive cycle and that the total loss during the spring outburst was 1·83 mg SiO_2. Hence the average loss was $\frac{1{\cdot}83}{2{\cdot}5 \times 7} \cdot 100 = 10\%$. For the productive period in May and June, we may compare the actual loss with the calculated loss, $\frac{N_c(P_1 - P_0).(R(m+1)-G)}{R-G}$, assuming that $N_c = 0{\cdot}14 \cdot 10^{-6}$ mg SiO_2 and arbitrarily that $m = 0{\cdot}1$:—

Month	*Week*	*Observed loss mg SiO_2/litre (from Table XIV)*	*Calculated loss mg SiO_2/litre*
May	1		
	2	0·10	0·155
	3	− 0·21	0·439
	4	0·36	0·583
	5	0·85	0·840
June	1	0·50	0·056
	2	0·12	0·067
	3		

Merely by using the observed values of P, R and G, the nutrient loss can be roughly calculated. It is likely that the decline in nutrients would be fairly well described with the formula $\frac{N_c(P_1 - P_0)[R(m+1)-G]}{R-G}$, when m is correctly specified.

The biological meaning of the formula is that the decline of nutrients depends upon the changing value of $R - G$, the balance between the algal reproductive rate and the algal mortality due to grazing. The primary agent in production is $R - G$ and any nutrient effect, for example, in reducing algal division rates partially or to zero, will arise as a secondary effect consequent on the loss of living material or of its breakdown products. The most interesting point is that if $R \simeq G$ over long periods, there would perhaps be no decline in nutrients. Consequently a constant low level of nutrients might imply that $R \simeq G$ and that most of the nutrient (as, for example, phosphorus) was perennially locked up in living material. A second point is that if nutrients are reduced, restraining the reproductive rate, there is a secondary control available which would be of primary importance if grazers were late or absent in the productive cycle.

III. THE ORGANIC PRODUCTION IN OCEANIC WATERS

III (i) INTRODUCTION

It was suggested in an earlier section that during the algal outburst the herbivores grazed in excess of their immediate needs. A consequence of the excess grazing would be that herbivores could subsist on faeces floating in the water during the apparently barren period after the spring outburst. Another consequence would be that an ample excess was provided

to supply the benthos, which would not be the case if the herbivores consumed all the algae in exact concordance with their needs.

In the model of plankton production (Section I) it was assumed that the algal reproductive rate need not be affected by nutrient lack: the model was constructed on the basis that the grazing capacity of the herbivores is a sufficient agent in reducing the algal stock. One of the consequences of the grazing capacity attributed to the herbivores was that a proportion of the nutrients was assumed to be regenerated immediately. Then the observed decline of nutrients was found to be adequately described in terms of the balance between algal reproduction and the grazing mortality of algae, so that production was never halted by nutrient lack. It was suggested as a corollary that if the algal reproductive rate and the grazing mortality of the algae were equal for a long time, no nutrient decline could take place. This would be a steady state system of production.

No seasonal decline of nutrients takes place in the tropics. The question arises whether tropical production is a steady state system, as opposed to the production in temperate seas and high latitudes, which is an unbalanced system. The third part of this paper is concerned with the seasonal and regional effects of the balance or unbalance of plankton production. For this purpose the available data from the Sargasso Sea have been examined.

The Sargasso Sea is best described as being in the centre of the main North Atlantic gyral and it is bounded to the south-west, west and north-west by the Antilles current, the Florida current and the Gulf stream respectively. The eastern boundary cannot be so readily defined, but for convenience, we will take it as the mid-Atlantic ridge.

There is a desert-like character which may be summarized in the following terms. The nutrients in the euphotic zone are found at very low levels indeed (Deacon, 1933; Seiwell, 1935; Rakestraw and Smith, 1937; Thomsen, 1937; Riley and Gorgy, 1948). As an apparent consequence, the standing stock of plankton is small (Hensen, 1911; Jespersen, 1924; Riley, Stommel and Bumpus, 1949). Because the plankton is sparse, the water is clear, the clearest in the world (Jerlov, 1951). Lastly, Steemann Nielsen (1952, 1954) has found a low rate of carbon assimilation in the Sargasso Sea.

III (ii) THE TROPICAL SEASONS

The seasonal variation in the extinction coefficients of underwater light in the Sargasso Sea is:—

Jan.-Apr.	*June-July*	*June*	*Aug.-Dec.*
0·059 to 0·066 (Clarke, 1939)	0·051 to 0·054 (Clarke, 1939)	0·42 (Steemann Nielsen, 1954)	0·42 to 0·047 (Clarke, 1939)

Jerlov (1951) showed that the extinction coefficient of tropical waters generally increased slightly in depth below 70 m and he attributed this to scattering of light by particles larger than 3 μ in diameter. As the extinction coefficients were greater in midwinter, it is likely that the productive season was then at its height (the winter flowering of Riley, Stommel and Bumpus, 1949). Table XV shows that this is probably true for the number of algae.

TABLE XV

Seasonal observations of algal standing stock in the Sargasso Sea (Riley et al., 1949; Riley, 1943; Riley and Gorgy, 1948)

	May	*June*	*August*	*December*
Number of observations .	5	3	5	9
Depth range . . .	0–400 m		0–400 m	0–200 m
P.P.U./m^2, 10^4 . . .	31	10	5	41·5

(*P.P.U.* is 1 Plant pigment unit.)

For zooplankton, Moore (1950) has shown that coelenterates, sagittae, pteropods and copepods were most numerous in the waters round Bermuda from December to June.

Thus, from three independent lines of evidence, it is likely that the productive season in the Sargasso Sea is in midwinter. Some confirmation of this thesis may be sought in a general examination of the productive season in different latitudes. Steuer (1902) and Cori and Steuer (1901) showed that the algal productive season in the Mediterranean extended from November to April; Bernard (1939) has described a production of nanoplankton off Monaco, extending from November to May.

In general, there appears to be a trend with decreasing latitude; in high latitudes, the algal outburst is fairly short and starts at midsummer or after (Hart, 1942; Digby, 1953) (in the Barents Sea, however, production starts in April in shallow water close to the ice (Marshall, 1958). In temperate latitudes, there is a spring and an autumn peak in the productive season, the first usually being the larger (Harvey, 1934). In low latitudes the spring and autumn peaks are continuous, leaving a sterile period in midsummer (Bernard, 1939). The same sort of pattern can be seen in the production of zooplankton (Digby, 1954, in Scoresby Sound; Herdman, 1919, in the Irish Sea; King and Hida, 1954, in Hawaiian waters).

As the equator is approached, so the productive season occurs earlier in the year. With this trend, another effect is noticeable—that the seasonal amplitude in the quantity of standing stock is less in low latitudes than in high. In low latitudes, the amplitude may be as low as five times, whereas in high latitudes it may be as high as fifty times. Thus, the winter production in the Sargasso Sea is not an isolated event, but part of a general pattern.

III (iii) NUTRIENTS IN THE SARGASSO SEA

There is no seasonal variation in the nutrient content in the Sargasso Sea (see Table XVI).

TABLE XVI

The distribution of phosphorus at different seasons in the Sargasso Sea
(Depth 0–100 m)

	February	*March*	*April*	*May*	*August*	*August*	*August*
μg.-at *P*/litre	0·060	0·100 0·040	0·080	0·020	0·125	0·000	0·075
Author	Seiwell (1935)	Seiwell (1935) Rakestraw and Smith (1937)	Seiwell (1935)	Riley (1939)	Seiwell (1935)	Thomsen (1937)	Riley and Gorgy (1948)

III (iv) THE STANDING STOCK IN THE SARGASSO SEA

Estimates of standing stock are rather rough, being derived from a few scattered observations. The equivalents used are as follows:—

1 P.P.U. = 3 — 5 μg C (Atkins and Parke, 1951; Riley and Conover, 1956).
1 g dried weight = 0·25 g C of mixed diatoms and dinoflagellates.
1 g dried weight = 0·44 g C of copepods. (Brandt and Raben, 1919–22).
1 g dry organic matter = 0·50 g C for copepods and algae (Brandt and Raben, 1919-22).
1 ml. displacement volume = 0·11 g dry organic matter. (Deevey, 1952). (zooplankton)

Phytoplankton

From the values in P.P.U. given in Table XV, the following averages are derived:—

Dec.–May: 1·44 – 2·39 g C/m² } 0–400 *m*
June–Aug. 0·30 – 0·50 g C/m² }

Zooplankton

With a Clarke Bumpus net in July and August, through a depth range of 0 to 400 m, Riley and Gorgy (1948) caught 0·05 ml displacement volume/m³, which is equivalent to 5·5 mg dry organic matter/m³ or 2·2 g dry organic matter/m². Off Bermuda, Moore (1950) used an N.70 net horizontally in half hour hauls at 2 knots and caught 30 mls displacement volume, which is equivalent to 0·042 ml/m³ or 0·005 g dry organic matter/m³. Over the depth range of 700 m this volumetric estimate becomes 3·5 g dry organic matter/m².

Combining the two sets of figures, the average annual value is 2·85 g dry organic matter/m² or 1·425 g C/m².

Macroplankton

Leavitt (1938) examined the catches from a 2 m net hauled horizontally at 2 knots for 2 hours down to 3200 m. Assuming that the net was only 30% efficient, he caught 1·7 g dry organic matter/m² at one station and 1·47 g dry organic matter/m² at the other; averaged, these estimates are 0·8 g C/m².

The deep scattering layer

The layer has been recorded to the south and south-west of Bermuda (Moore 1950; Hersey *et al.* 1952). The signals were comparable in amplitude to those received from shrimps at the very high density of 20/m³ and they extended in depth for 100 m (Hersey *et al.* 1952).

1 euphausiid weighed 22·2 mg dried weight (Cushing and Corlett, unpublished). So the deep scattering layer, based on the estimates of Hersey *et al.*, consists of 44 g dried weight/m².

If the layer is really composed of fish, much of the transmitted sound energy would be scattered back from the air bladder. Cushing and Richardson (1955) estimated that the signal from the air bladder was 40 to 70% of the total signal from fish and air bladder. A reasonably safe estimate of living material in the deep scattering layer would be 5 to 10 g dried weight/m².

Comparison of the standing stock in the Sargasso Sea with that in the English Channel

Table XVII has been compiled using Harvey's estimates (1950) and those given above.

Table XVII

Standing stocks in the English Channel and in the Sargasso Sea in g dry weight/m²

	Phytoplankton	*Zooplankton*	*Macro-plankton*	*Pelagic fish*	*Benthos*	*Demersal fish*
English Channel .	4	1·5	—	1·8	17	1·125
Sargasso Sea .	0·36 to 2·32 0·60 to 8·32	2·2 to 3·5	1·58	5–10		—

The difference between the Channel and Sargasso Sea observations is one of depth, 70 m in the Channel and 400 m in the Sargasso (3200 m for the macroplankton), so any measurement of standing stock/unit volume in the Channel may be five times that in the Sargasso and still lead to the same estimate per unit surface.

Perhaps the most interesting point emerging from Table XVII is that the benthos and demersal fish of the continental shelves may be replaced ecologically in the oceans by the organisms constituting the deep scattering layer. If this were so, it might be expected that the layer consisted of two parts, firstly the pelagic fish feeding on plankton and macroplankton and secondly scavengers that feed on detritus and organic material. There are detritus-feeding euphausiids (Marshall, 1952) which might well fill this latter role, and which would also provide food for pelagic fish in addition to the plankton.

It is possible that the whole productive cycle in the ocean takes place clear of the bottom, with the exception of some *Foraminifera* and some *Radiolaria*. Both the scavengers and herbivores would migrate towards the surface at night, so there is the greatest possibility of regeneration taking place in the euphotic zone—in fact, it is possible that the scavenging animals may partly feed in deep water and excrete near the surface.

III (v) RATES OF PRODUCTION

(a) Phytoplankton production

Using the C^{14} method in the Sargasso Sea, Steemann Nielsen (1954) found the following rates of carbon production in June: 0·043, 0·058 and 0·048 *g* C/m²/day. At this time, from Riley's observations, the standing stock of algae might have been 0·25 to 0·50 *g* C/m² (see Table XV), which is an overestimate because chlorophyll was used. Hence the coefficient of productivity: $\frac{\text{rate of C produced/day}}{\text{standing stock in C}}$ may have been about 10 to 20%/day. The samples of standing stock were taken down to 400 m and the euphotic zone extended to about 120 m, so the coefficient of productivity should perhaps be increased by 2 to 3 times; an average value of 40% fits with analogous observations made in the North Sea (Cushing, 1957) and with the theoretical values given in the earlier part of this paper. It is worth pointing out that in June, the nutrient observations are very low (about 0·06/μg—at *P.*/litre.).

(b) Grazing of the herbivores

A herbivore as large as an adult *Calanus* would sweep clear 2,500 mls/day, on the encounter theory of grazing, in the Sargasso Sea, if all algae were of 2,000 μ^3 in volume, which is probably a little large.

Let 1 adult *Calanus* weigh 0·59 mg wet weight

$$= 0{\cdot}06 \text{ mg dried weight (Riley } \textit{et al.} \text{ 1949).}$$

Then the standing stock of 2·85 g dried weight/m³ of herbivores is equivalent to 47,500 adult *Calanus*/m². This is an overestimate because it includes some carnivores, but it would amount to 0·12 *Calanus*/litre in a depth of 400 m.

The grazing mortality of the algae is 2,500 × 0·12 = 300 mls/day or 0·3, using 1 litre as the unit of volume.

In summer there is 0·60 g dried weight/m² of algae, which is 15.10^{-4} mg dried weight/litre. So each *Calanus* is taking 3·75 μg/day or one sixteenth of its own weight. In winter time, at the higher value of algal standing stock, each animal would be taking one fifth of its own weight/day.

(c) Comparison of the algal reproductive rate with the herbivore grazing rate

A reproductive rate of 0·2 to 0·4 and a grazing rate of about 0·3 means that the two rates are approximately balanced. Although this is only the roughest of estimates, the implication is that the productive cycle might well be approaching a steady state system. It is likely that the herbivores in this system get enough to eat despite the fact that size differences and temperature differences have not been taken into account; as tropical herbivores are smaller than *Calanus* and the water is warmer, the two new effects would counter each other—a smaller animal would sweep clear a smaller volume, but this would be increased at a greater temperature.

The seasonal amplitude in algal standing stock is small, therefore the difference between R and G cannot change rapidly as it does in temperate seas. If R and G are really balanced, then it is likely that there will be little seasonal variation in nutrients, as shown in Table XVI.

III (vi) THE FULL PRODUCTIVE CYCLE

The productive cycle may be formulated in the following way:—

Trophic level	
I Nutrients	$\frac{dN}{dt} = (R_n - U_n)\,N$
II Phytoplankton	$\frac{dP}{dt} = (R_p - G_h - M_p)\,P$
III Herbivores	$\frac{dH}{dt} = (R_h - G_f - M_h)\,H$
IV Herbivore-feeding fish	$\frac{dF}{dt} = \{(\overline{I_f - E_f}) - (G_t + M_f)\}\,F$
V Fish-feeding fish	$\frac{dT}{dt} = (\overline{I_t - E_t})\,T$

where N is the quantity of algal nutrients,

P is the quantity of algae,

H is the quantity of herbivores,

F is the quantity of herbivore-eating fish,

T is the quantity of fish-eating fish;

(all quantities are expressed as per unit volume or beneath unit surface).

R_n is the daily regeneration rate of nutrients,

R_p is the daily reproductive rate of the algae,

R_h is the daily reproductive rate of herbivores,

$(\overline{I_f - E_f})$ is the balance between immigration and emigration rates of herbivore-feeding fish.

$(\overline{I_t - E_t})$ is the balance between immigration and emigration rates of fish-feeding fish,

U_n is the daily uptake rate of nutrients,

G_h is the daily grazing mortality rate of algae due to herbivores,

G_f is the daily grazing mortality rate of herbivores due to herbivore-feeding fish,

G_t is the daily grazing mortality rate of fish due to carnivores;

M_p is the daily 'natural mortality' rate of algae,

M_h is the daily 'natural mortality' rate of herbivores,

M_f is the daily 'natural mortality' rate of herbivore-feeding fish;

t is time.

The dependences between the trophic levels are established in the herbivore/phytoplankton relation: the dependence of the herbivore reproductive rate on the algal standing stock and the dependence of the algal grazing mortality rate on the herbivore standing stock. The other dependences are formally analogous to these two basic types. Although they are the necessary links connecting the trophic levels in the formulation given above, there is no evidence on the precise form of other dependences.

A distinction has been made between herbivore-feeding fish and fish-feeding fish, because there is a place in the deep oceans for tunny, giant squid and carnivorous whales. The aggregation and disengagement of both groups of fish is assumed to be effected by a balance between immigration to and emigration from the area of a particular food patch.

There are two extreme types of the productive cycle; the first is the steady state and the second is the unbalanced one. When the whole productive cycle is in the steady state, each equation at each trophic level would equal zero, i.e., the exponents are balanced and the standing stock does not change. Excluding the 'natural mortality', the balance may be shown symbolically in the following way:

$$N_1 = N_0 \cdot e^{(R_n - U_n)(t_1 - t_0)}$$

$$P_1 = P_0 \cdot e^{(R_p - G_h)(t_1 - t_0)}$$

$$H_1 = H_0 \cdot e^{(R_h - G_f)(t_1 - t_0)}$$

$$F_1 = F_0 \cdot e^{(I_f - E_f) - G_t(t_1 - t_0)}$$

The most important condition for the steady state productive cycle is that the regeneration of nutrients takes place quickly and continuously at all levels. Herbivores and both types of fish all migrate towards the surface in darkness and because populations from 2,000 m are concentrated in the top 100 m, there is every possibility that regeneration takes place by excretion in the depth of the euphotic zone, as mentioned above.

The converse of the steady state is the fully unbalanced one, in which full production takes place at each trophic level in succession, starting with the algae. Consequently, R_n, the rate of nutrient regeneration, G_h, the rate of algal grazing mortality, G_f, the rate of herbivore grazing mortality and G_t, the rate of fish grazing mortality, do not appear. This does not mean that regeneration and grazing do not take place, but that they take place only after the peak of production at each trophic level has been passed; consequently, there are no linking dependences from these parameters to the standing stocks. In other words, the grazing on the algae does not begin until all nutrients have been used up and the maximum standing stock is equivalent to maximum production. A formulation of the unbalanced state in time is as follows:—

$$N_1 = N_0 \cdot e^{U_n (t_1 - t_0)}$$

$$P_1 = P_0 e^{R_p (t_2 - t_1)}$$

$$H_1 = H_0 e^{R_h (t_3 - t_2)}$$

$$F_1 = F_0 e^{\overline{(I_f - E_f)}(t_4 - t_3)}$$

$$T_1 = T_0 e^{\overline{(I_t - F_t)}(t_5 - t_4)}$$

——————————————————→ time

Once the algal division rate is released from darkness and turbulence, algal production is limited only by nutrient concentration. When algal production stops at the maximal standing stock, grazing starts and the zooplankton is allowed to reproduce at a maximum rate, subsequently diminishing. Similar events take place at the higher trophic levels; the difference between the unbalanced and the steady state is that grazing does not modify production as it proceeds, since the regeneration of nutrients does not take place at first. However, this must occur as grazing gets under way and so some production can then take place as R and G both diminish.

DISCUSSION

A discrepancy was found between the food required by *Calanus* and the food that the animal apparently obtained in grazing experiments. Experiments of a different type, using large vessels, showed that the quantities grazed were high enough to supply the animal's metabolic needs to excess; these values corresponded to field estimates made off the north-east coast of England (Cushing, 1955).

A plankton model was developed using a theoretical algal reproductive rate and a theoretical grazing rate. There are three reasons for suggesting that these rates are approximately correct:—

1. Division rates estimated both from Lund's data and Jenkin's data were close to those observed at sea in April 1949, using another method.
2. An encounter theory of grazing was developed which has been shown to be of the right order as confirmed by recent preliminary experiments.
3. If R and G were correctly estimated, the approximate fit of the plankton model to the observations can only mean that other factors, which must be numerous, are possibly of less importance than the primary ones, R and G.

If production were really controlled by the balance of these two primary factors, then the part played by nutrients had to be re-examined. If grazing limits production before nutrient lack, why do nutrients decline as production increases? It was assumed that the uptake of nutrients was proportional to production and that the quantity grazed was proportional to immediate regeneration. In terms of the theoretical model developed from these assumptions, it was shown that the decline in nutrients was proportional to the loss in nutrient from the productive processes as a result of the unbalanced processes of production. If grazing is excessive during the spring outburst the regeneration of nutrients may well roughly balance their uptake and this balance shifts only after the peak of production. Thus, the decline in nutrients is really a symptom of production and although the nutrient lack may subsequently halt production, it does not necessarily do so.

Riley and Gorgy (1948) have already pointed out that the standing stock in the Sargasso Sea when expressed as 'beneath unit surface' is comparable in quantity to that found in the English Channel. There are three new points:—

1. the occurrence of the productive season in winter or in early spring;
2. the replacement of the benthos of the continental shelf by the deep scattering layer, which probably feeds and excretes at the surface at night;
3. the numbers of plants and herbivores are probably sufficient to allow the herbivores to get enough to eat.

Common to all three factors is the implication that uptake of nutrient is balanced against regeneration, that algal reproduction is balanced against grazing. Two forms of productive cycle were formulated, the steady state cycle and the unbalanced cycle. The first is probably found in tropical waters and the second in high latitudes and neither is likely to exist in a pure state.

It is not known which of the two forms of cycle is the more productive, because many of the parameters cannot yet be estimated. We can, however, say that tropical seas are not necessarily marine deserts merely because the nutrient salts are apparently in short supply.

We can also say that the most important effect in the high temperatures of tropical seas is that the breakdown of dissolved organic material will be much accelerated. Effectively this would free the largest component of loss in temperate waters. Consequently, the other component, that locked up in living organic material, would become the largest component of loss. These are effects which increase the probability of a steady state system; it is likely that the temperature coefficient of the breakdown rate is one of the factors that determines the degree of balance in the productive cycle.

It may be noted that it is the low temperature that makes the regions of upwelling abnormal. It is possible that the low temperature and turbulence reduce the algal division rate and the breakdown rate sufficiently to render the cycle unbalanced, producing a high standing stock, at the same place as upwelled nutrient, which bears little relation to the production taking place.

Because I have tried to account for the general patterns of production in terms of a balance between algal reproductive rate and herbivore grazing rate, it appears that the direct role of nutrients in production has been underestimated. The first reason for this was that the evidence for a reduction in algal reproductive rate at low nutrient levels was slender. The second reason was that although herbivores were apparently often starved, the role of grazing had up till now been neglected. There is no evidence that either factor is dominant, but in this paper I have taken the view that grazing is the dominant factor for the purpose of exploring theoretical possibilities. Then the restriction of the algal reproductive rate due to nutrient lack plays a secondary but necessary part, stopping production in the absence of grazers, in time or space.

For a model of production combining both effects, the relation between algal reproductive rate and nutrient concentration must be more clearly established and the exact mechanism of grazing must be determined.

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